The Mentalities of
Gorillas and Orangutans

Comparative Perspectives

Edited by

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Hominid family values: morphological and molecular data on relations among the great apes and humans.

DAVID R. BEGUN

"What we've got here is, failure to communicate." (Cool Hand Luke. Warner Bros., 1967)

INTRODUCTION

Recent fossil discoveries, methodological advances, and ongoing analyses of hominoid comparative molecular biology and morphology have led to dramatic changes in our current understanding of relations among the great apes and humans. The late nineteenth-century view of these relations held that humans and the African apes were most closely related, and that the Asian great ape, the orangutan, was a more distant relative (Darwin, 1871; Huxley, 1959). For most of the twentieth century however, the great apes have been placed not only in their own family (the Pongidae), but also in their own separate evolving lineage, to the exclusion of humans. In the past thirty years, a few molecular biologists have been questioning the evolutionary reality of the pongid lineage, suggesting a return to the Darwin–Huxley view, placing African apes closer to humans, but based on the results of comparative molecular biology. During that time, the techniques of molecular systematics have been greatly improved and refined, to the point where researchers are today actually comparing nucleotide sequences, the fundamental, specific arrangement of DNA molecules, as opposed to overall DNA similarity (hybridization) or the products of DNA metabolism (proteins).

This work in molecular biology has been joined by recent developments in method and theory in palaeontology and comparative anatomy. Foremost among these is the widespread adoption of cladistic methodology, but other developments include more comprehensive analysis of hominoid comparative anatomy, and a more complete hominoid fossil record. One of the outcomes of this revolution in hominoid systematics is the perception that a great divide exists between "traditional" and "modern" hominoid classifications, and that the former has or inevitably will be replaced by the latter. We could switch the words "traditional" with "morphological," and "modern"

with "molecular," reflecting the widely held view, even among some morphologists, that, in systematics, molecules have priority over morphology (e.g., Gould, 1985). The fact is, however, that morphology-based hominoid systematics has progressed enormously during the time in which molecular systematics has been coming into its own. Since the 1980s, new discoveries and the standardization of approaches to phylogeny reconstruction have made morphological systematics quite distinct from earlier research. Unfortunately the "phylogenetic baggage" of a century or more of work in hominoid systematics, often of very high quality, has made some researchers doubtful of their own results (e.g., Groves, 1986; Pilbeam, Rose, Barry, & Shah 1990; Pilbeam, 1996). In contrast, the impressiveness of recent advances in molecular techniques, which currently allow the relatively quick sequencing of nuclear genes and complete mitochondrial genomes in multiple individuals, may have produced some excess of confidence in the potential of molecular approaches to yield the "right" answer (e.g., Gould, 1985; Easteal, Collet, & Betty, 1995). What is needed in this area of research is more communication between the practitioners of both approaches. There is more disagreement within molecular systematics and within morphological systematics than between the two (see below). Compared to the conclusions of hominoid systematics through the 1970s, the conclusions of morphologists and molecular systematists today are much closer than they are divergent. So, rather than focusing on the so-called morphology vs. molecules debate (Patterson, 1987; Cartmill & Yoder, 1994; Shoshani, Groves, Simons, & Gunnel, 1996), this chapter highlights the significant amount of consensus between these fields that has been emerging in the past five years.

In an attempt to move away from the morphology–molecule dichotomy, this chapter is organized along research questions rather than methodology. The main question is, what are the evolutionary relations among living great apes and humans? We can resolve this big question into a series of smaller issues given the results of research over the past century and a quarter. These are, from the phylogenetic perspective: What is hominid, nowadays? What is an orangutan, anyway? How are African apes and humans related to each other? The last question is the most complex, and has generated the most controversy, particularly with regard to the issue of how humans fit in. Before coming to these questions, however, one approach common to both molecular and morphological systematics, cladistics, is outlined, as it has had perhaps the most profound influence on this field of any development in modern systematics.

BACKGROUND TO CLADISTIC APPROACHES

A cladistic approach to systematics is simply one in which the only information considered relevant to the classification of organisms is commonality of descent. Organisms share characteristics of external appearance, genetics, morphology, and behavior for a number of reasons, only one of which is directly attributable to the pattern of their evolutionary relationships (see below). Because a classification of organisms must be derived from phylogenetic conclusions deduced from observations of traits organisms share, the method and theory of classification focuses primarily on

distinguishing phylogenetically informative characters, or *shared derived characters* (*synapomorphies*) from others (see below). Systematics is not palaeobiology or neontology. It is simply classification, which helps to organize and standardize the database of organisms known to humans, and allows or facilitates communication among colleagues. It does not seek to characterize organisms in any way beyond their evolutionary relations. The more interesting qualities of organisms are fleshed out in studies of ecology, behavior, evolution, and adaptation.

This view of the role of systematics is not universal (Hull, 1979), but it is becoming more common. Given this limited goal, cladistics can be viewed as a well-defined protocol for determining evolutionary relationships. Although there have been many refinements, the primary reference to cladistic methodology is Hennig (1966). While many of the ideas proposed by Hennig were already part of mainstream systematics (e.g., Simpson, 1961), Hennig standardized the approach to systematics that is nearly universally accepted today, providing a well-defined, if slightly cumbersome, vocabulary (Table 1.1), and a straightforward methodology.

One important limitation of the cladistic approach is the fact that it is incapable of providing evidence for ancestor–descendent relationships. In fact, it seeks only to find what are referred to as sister group relations. Sister taxa are those which share a common ancestor not shared by any other organism, that is, taxa that are more closely related to one another than they are to anything else. Establishing closeness of relationship is a matter of identifying character states[1] shared only by sister taxa, which are most easily explained as having been passed on to these taxa from a common ancestor. Thus, in the process of identifying sister taxa, a set of ancestral character states, or ancestral morphotype, is assembled, but a specific ancestor cannot be identified. At best, one could say that a known taxon does not differ from a reconstructed ancestral morphotype and is a candidate for the ancestry of another taxon. *Ardipithecus ramidus* (White, Suwa, & Asfaw, 1994), for example, appears to conform very closely to the reconstructed ancestral morphotype for the human lineage, but cannot technically be identified as an ancestor using this approach (Figure 1.1). An hypothesis of ancestor–descendant relationship is one that includes a processual component, some statement that involves time, selection, adaptation, environmental change or any combination of these (Figure 1.1). Sister relationships are much simpler hypotheses, involving only pattern recognition. A cladistic approach to systematics thus produces a cladogram, or dendrogram of relations, which can be viewed as the skeleton upon which an hypothesis of phylogeny (including ancestors and descendants) is fleshed out.

In a nutshell, sister relations are determined by identifying shared character states derived from the last common ancestor of the set of taxa under analysis. In order to carry out this type of analysis, taxa must be compared to other taxa known to be outside their evolutionary lineage, that is, an outgroup. This is a necessary initial assumption, but it is usually fairly straightforward. Outgroups are usually taxa most closely related

[1] Character states are specific configurations of a character. For example, in hominoids the character "os centrale" has the character states "separate" and "fused to the scaphoid."

Table 1.1 *Cladistic terminology used in this chapter*

Autapomorphy	Uniquely derived characters, having evolved since the divergence of a taxon from its **sister taxon**.
Characters	Units of analysis in phylogeny reconstruction.
Character States	The condition of a character in a taxon (large, small, pronounced, weak, etc.).
Clade	An evolutionary lineage, and the unit of an evolutionary classification.
Homology	Shared characters and/or character states having been inherited from a common ancestor.
Homoplasy	Shared characters and/or character states having been inherited independently from a common ancestor (parallelism) or from different ancestors (convergence).
Monophyletic taxon	A taxon having evolved from a common ancestor. A monophyletic taxon normally includes all descendants of that common ancestor, and is identified on the basis of its **synapomorphies**.
Outgroup	A relative of the group of organisms under analysis, usually the **sister taxon**, used to determine the **polarity** of **character states**.
Paraphyletic taxon	A taxon that excludes some of the descendants of a common ancestor. Paraphyletic taxa are usually identified on the basis of **symplesiomorphies**, and not considered valid evolutionary taxa by cladists.
Polarity	The evolutionary significance of a character state, either apomorphic (derived) because it is not present in the outgroup, or plesiomorphic (primitive) as indicated by its presence in the outgroup.
Polyphyletic taxon	A taxon with multiple ancestors, usually based on homoplasies. Polyphyletic taxa are infrequently identified today.
Sister taxon	The closest relative of a taxon, usually at the same hierarchical level (species, genera, families, etc.).
Symplesiomorphy	Shared primitive character state also found in the **outgroup** and presumed to have been inherited from a common ancestor with the outgroup and not from the last common ancestor of the taxa under analysis.
Synapomorphy	Shared derived characters, not found in the **outgroup** and presumed to have been inherited from the last common ancestor of the taxa under analysis.

Source: Hennig, 1966.

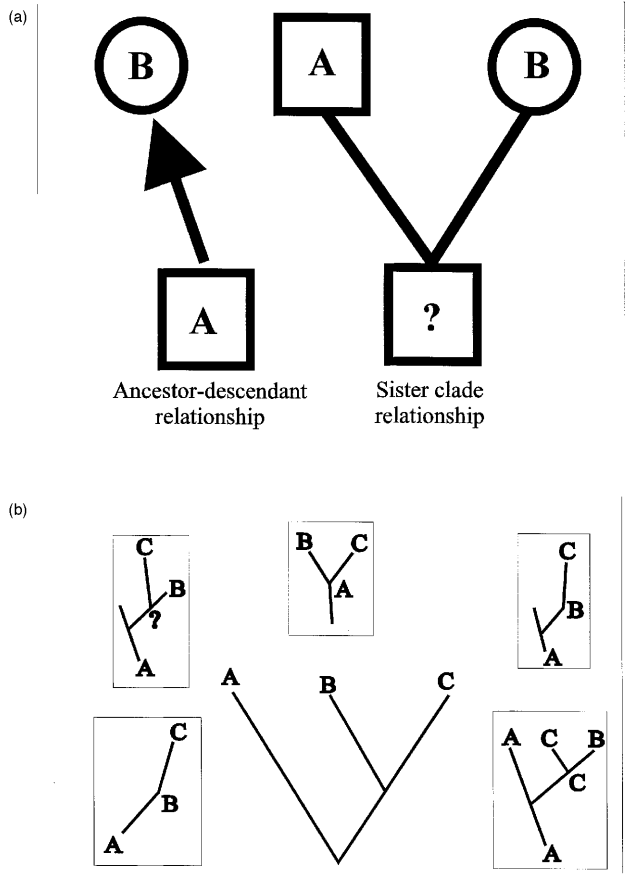


Figure 1.1 Phylogenies and cladograms.
(a) A phylogeny (left) depicts ancestor–descendant relationships. An ancestor–descendant hypothesis requires support from data directly related to the interpretation of evolutionary relationships (morphology, molecular biology, behavior, etc.) as well as information on the process of evolutionary change and the passage of time, represented by the arrow. A cladogram (right) simply represents a hierarchy of evolutionary relationships, without regard to the specifics of the process responsible for the observed diversity. Cladistic hypotheses are thus simpler but less comprehensive than phylogentic hypotheses, and should always precede the latter.
(b) A cladogram surrounded by five alternative phylogenies. Each phylogenetic hypothesis is consistent with the cladogram. Clockwise from the left: a unilinear hypothesis; the ancestors persists following two divergences, with the common ancestor of B and C unknown; B and C diverge for A; A and the common ancestor of B and C are briefly contemporary, and then B evolves into C; A, B, and C persist to the present following a divergence of the common ancestor of B and C from A and then B from C. Many other phylogenies are also consistent with this single cladogram. Deciding among them requires information on adaptation, selection, paleoenvironment, relative dating, and other paleontological variables.

to the set of taxa under analysis, but not included among these taxa. For catarrhines, the outgroup is widely viewed to be platyrrhines, for the Hominoidea, there is little dispute in recognizing the Cercopithecoidea as the outgroup, and for hominids it is widely viewed as hylobatids (see below). In order to identify character states that were present in the last common ancestor of living catarrhines, the outgroup, in this case platyrrhines, is examined for these traits. If catarrhine character states are found in platyrrhines, the most obvious explanation is that they come from a more ancient ancestor shared by both platyrrhines and catarrhines. For example, many catarrhines have tails and fore and hindlimbs of roughly equal length, moderate encephalization compared to prosimians, large canines, well-developed snouts, and divergent halluces. All of these traits are also found in most platyrrhines, and so it can be deduced that these were present in the common ancestor of platyrrhines and catarrhines and do not therefore serve to distinguish catarrhines and platyrrhines. These are *shared primitive characters*, or *symplesiomorphies*. Many or all catarrhines also have two premolars, an ossified ectotympanic tube, some reduction in the tail, and no humeral entepicondylar foramen. These character states are not found or are not common in platyrrhines, suggesting that they appeared in the ancestor of the catarrhines after it diverged from the ancestor of the platyrrhines. These would be shared derived characters of the catarrhines. However, because platyrrhines have also evolved since the appearance of their last common ancestor, it is possible that character states not found in platyrrhines have been lost or modified from their ancestral condition. Thus, it is advisable to look to the next available outgroup to confirm the conclusion that these character states are indeed derived. As it happens, many fossil and living prosimians also resemble platyrrhines in lacking most of these character states, although one of them, tail reduction, is ambiguous. In this case, it seems that catarrhines retain a simpler tail from a more ancient ancestor, while many platyrrhines have evolved more elaborate tails.

The method outlined above, using an outgroup to establish whether character states typical of the ingroup are primitive or derived (i.e., the polarity of character states), is called the outgroup criterion, and it is by far the most common. This is due to its relative simplicity, though a few assumptions are required. The most important assumption concerns *homology*. It is assumed that character states that are identified as the same in different taxa are homologous, that is, that they are the same character in an evolutionary sense, having evolved once in a common ancestor and having been retained little modified in descendants. This is a necessary initial assumption, and it is also fairly safe, from a methodological standpoint, for two reasons. The assumption of homology is falsifiable. The pattern of derived character states found in ingroup taxa need not conform perfectly to the pattern of relationships deduced from it. A minority of characters will always be inconsistent with the pattern of relationships suggested by most of the characters. These inconsistent characters are considered *a posteriori* to have arisen independently, by convergence or parallelism, and are thus identified as *homoplasies*. The assumption of homology, which was necessary to deduce a pattern of relationships, is falsified for these characters. The other strength of the assumption of homology is parsimony. It is more parsimonious to assume that a character state arose once

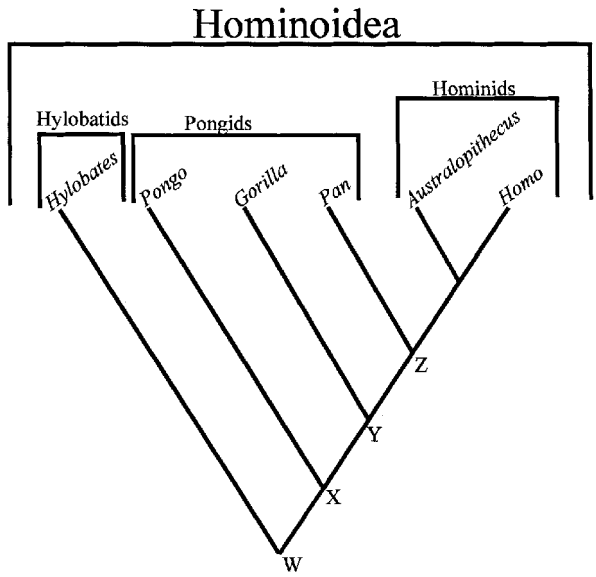
than to assume that it arose independently more than once. Parsimony, however, is not a description of the evolutionary process. In fact, as just noted, cladistic analyses always reveal homoplasies, which demonstrates the degree to which evolution is not parsimonious, that is, the frequency with which similar character states arise by multiple pathways. Parsimony is a point of logic only. It simply refers to the longstanding preference in science for simpler explanations over more complex ones. All else being equal, a simpler explanation is to be preferred, so long as it does not violate well-established principles. Cladistics has been criticized for representing evolution as parsimonious (most recently in Marks, 1994), but this misunderstanding could not be further from the truth. Cladistic analysis, ironically, has revealed more parallelism and convergence among organisms than had previously been thought possible, reinforcing the notion of the enormous complexity of the evolutionary process.[2]

The final goal of a cladistic analysis is the hierarchical representation of *monophyletic* clades, the cladogram. Strictly monophyletic clades are lineages which include all the descendants of a single ancestor. Another way of describing monophyletic clades is that they contain taxa that are all more closely related to each other than to any taxon in another clade. In contrast to monophyletic clades, *paraphyletic* clades exclude some descendants, or they group together taxa some of which are in fact more closely related to outsiders than to others in the clade (Figure 1.2). In the hominoids, for example, Pongidae is paraphyletic when used in the traditional sense because it excludes humans even though humans are more closely related to some pongids (African apes) than these pongids are to other pongids (orangutans). Pongidae would be monophyletic if it included humans, but humans are designated as hominids, which has taxonomic priority[3] over pongids, so that the correct nomen for this monophyletic clade is Hominidae (see below). Recognition of this paraphyly has lead many systematists to reject the nomen Pongidae. In contrast, paraphyly in other hominoids has lead to an increase in nomina. The traditional use of the nomen *Australopithecus* (including all non-*Homo* fossil humans) is also paraphyletic, because it excludes *Homo* despite the fact that *Homo* is more closely related to some *Australopithecus* than some species of this genus are to others in the same genus. The trend here has been to recognize other distinct genera (*Ardipithecus*, *Paranthropus*) thereby removing them from the *Australopithecus* clade.

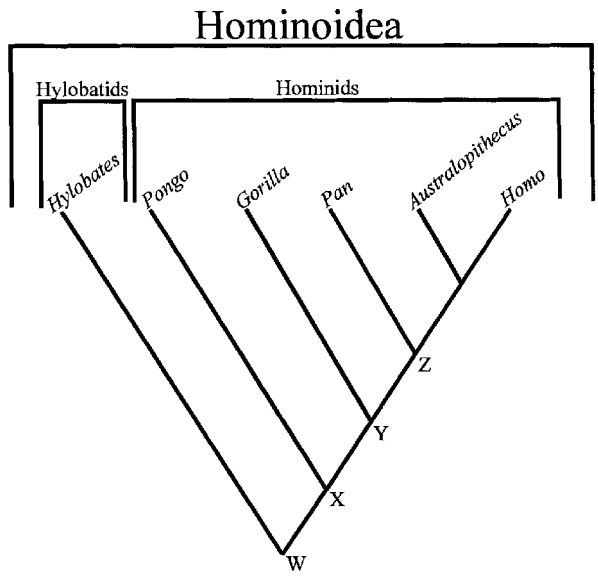
[2] Other methods of identifying derived character states have been proposed. These include palaeontological and ontogenetic criteria, which rely on the order of appearance of character states in the fossil record or in individual growth and development to polarize character states. Because of the additional assumptions these criteria require, concerning the process of ontogeny and the degree to which it accurately reflects evolutionary relations, and the relative completeness and reliability of the fossil record, these approaches are much less commonly used than the outgroup criterion. In this chapter, nearly all the described research proposing various evolutionary relations relies on the outgroup criterion.

[3] Taxonomic priority is a simple but essential rule of taxonomic nomenclature. It requires that taxa considered to be the same be designated by the first used nomen. In this case, since great apes and humans belong in the same family (see below), the first used family nomen Hominidae has precedence. This rule prevents the inevitable confusion that would arise from using different "preferred" nomina to describe the same taxon.

(a)


Hominoidea
Hylobatids
Pongids
Hominids
Hylobates
Pongo
Gorilla
Pan
Australopithecus
Homo
Z
Y
X
W

(b)


Hominoidea
Hylobatids
Hominids
Hylobates
Pongo
Gorilla
Pan
Australopithecus
Homo
Z
Y
X
W

Though cladistics was developed and refined by neontological morphologists, it is now widely used by both paleontologists and molecular systematists. The methodology is the same in all areas of research. Character analysis uses the outgroup criterion to polarize character states. Parsimony analysis determines the branching sequence requiring the fewest number of independent origins of character states while still being consistent with the largest number of characters. The remainder of this chapter surveys the recent literature on hominoid systematics, and reviews some of the implications for understanding the evolutionary history of some of the more basic attributes of living great apes and humans.

WHAT IS A HOMINID, NOWADAYS?

A consensus has been achieved among systematists today that the family Hominidae includes more than the genus *Homo*, which was the case when the term was coined. But which additional taxa are allowed to enter the hominid club is the subject of some debate. Although it was not immediately clear to any researcher that *Australopithecus* should be classified as a hominid (Dart, 1925; Woodward, 1925; Keith, 1931), the hominid status of *Australopithecus* soon became widely accepted (Le Gros Clark, 1934). Simpson (1945), in his classic work on mammalian systematics, separated humans and their fossil ancestors, the Hominidae, from all apes, which he placed in the Pongidae. Today, the overwhelming majority of researchers working on hominoid systematics would include some or all of the great apes among the hominids. Widening the definition of hominids was first proposed convincingly based on immunological distances (Goodman, 1963). Goodman (1963) suggested that the African apes should be grouped with humans in the Hominidae, reflecting the closer evolutionary relationship among African apes and humans than between them and either orangutans or hylobatids. As Goodman (1963) noted, this view mirrors that of Darwin (1871), who concluded that it was likely that humans are more closely related to African apes than to

Figure 1.2 (*Opposite*) Monophyletic and paraphyletic taxa.
Pongid is a paraphyletic taxon because it includes the African apes and excludes humans, even though African apes and humans are more closely related to each other than either group is to orangutans. Another way of looking at this is that pongid is paraphyletic because it does not include all the descendants of the common ancestor of included taxa. In this case, Y and Z must be pongids because they are ancestors of the African apes and they postdate the common ancestor of the pongids (X), yet the pongids as defined here do not include all the descendants of Y and Z (the hominids are excluded). Separating hominids and pongids also fails to recognize the close evolutionary relationship among these taxa compared to hylobatids.
A simple monophyletic solution to the paraphyly of the pongids. As defined here, the hominids unites all the great apes and humans in a single family, and also serves to communicate their close evolutionary ties. All hominids have the same evolutionary relationship to hylobatids, and all the descendants of earlier hominids are included in the taxon. Note as well that the stem hominoid (W) is neither a hylobatid nor a hominid, because if it were one of these, that taxon would become paraphyletic. This illustrates one of the methodological limitations of cladistic analysis in recognizing ancestor–descendant relationships.

Asian apes. Goodman and colleagues (Goodman et al., 1989; Bailey, et al., 1992; Goodman et al., 1994) have recently gone one step further in proposing that the hominids should also include all living hominoids, including the hylobatids (gibbons and siamangs). In a reversal of the more usual order in which revisions are proposed in hominoid systematics, the conclusions of Goodman and colleagues concerning hylobatids corresponds to the previously proposed classification of hominoids provided by Szalay and Delson (1979), based almost exclusively on morphological data. Other researchers who use family-level taxonomic categories (most avoid the taxonomic issues and concentrate on phylogeny) continue to separate hylobatids from hominids (e.g. Groves, 1993; Wilson & Reeder, 1993; Hayashi et al., 1995).

The molecular work proposing a redefinition of the Hominidae was eventually followed by morphological support (Delson & Andrews, 1975; Szalay & Delson, 1979). Though it is fair to say that the acceptance of this revision was slow among palaeontologists and palaeoanthropologists specifically interested in hominoid systematics (e.g. Simpson, 1963; Ciochon, 1983; Fleagle, 1988; Martin, 1990), it was relatively quickly accepted by many morphologists and molecular systematists (e.g., Andrews & Cronin, 1982; De Bonis, 1983). Simpson (1963), Ciochon (1983), Fleagle (1988), and Martin, (1990) all in fact agree with the phylogenetic hypothesis proposed by Goodman (1963), but prefer to retain Hominidae for humans and their ancestors, to communicate the uniqueness of humans, and to maintain a certain amount of stability in hominoid nomenclature. While there is something to be said for stability, stability at the expense of an accurate representation of evolutionary relationships has long been rejected in systematics (e.g., Darwin, 1859; Simpson, 1961; Hennig, 1966; Hull, 1979; Brooks & McClennan, 1991). An overemphasis on taxonomic stability results in more confusion than that which arises from the periodic changing of nomina to accommodate strongly supported phylogenetic revisions.

More recently, the Hominidae has been expanded to include the orangutan and its fossil relative *Sivapithecus* (Andrews, 1985). This is currently very widely accepted, especially among researchers working on great ape systematics and relationships among great apes and humans (Tattersall, Delson & Van Couvering, 1988; Groves, 1989; Andrews, 1992; Begun, 1992a, 1994a; Perrin-Pecontal, Gouy, Nignon & Trabuchet, 1992). Most recently, other diagnostically great ape taxa from the Miocene (*Dryopithecus*, *Ouranopithecus*, *Lufengpithecus*, and *Oreopithecus*) have also been added to the list of known hominids (Begun, 1994a; Begun, Ward, & Rose, 1997).

The one area in which a strong reluctance to include great apes among the hominids persists is Plio-Pleistocene hominid research. Researchers working on Pliocene hominid fossils most commonly refer to these specimens as "early hominids" (Leakey, Feibel, McDougall, & Walker, 1995; White et al., 1994; Bromage & Schrenk, 1995), "basal hominids" (White et al., 1994), or even "the oldest hominids" (Wood, 1994). Two recent papers however point to a possible change in this dichotomy between researchers on hominoid systematics and those who work primarily on fossil humans. Aiello and Wood (1994) use the term hominine (an informal subfamily designation) for fossil and living humans, suggesting that the great apes are to be included with humans in the

Hominidae, though they do not use this latter term. Lieberman, Wood, and Pilbeam, (1996) in their analysis of phylogenetic relations among fossil humans, appear conscious of this discrepancy as well, and are consistent in their qualification "Pliocene hominids," suggesting that earlier or other hominids may exist. My sense from these published indicators and from conversations with Plio-Pleistocene fossil hominid researchers is that the more narrow, traditional definition of the Hominidae will disappear in the near future. Slowly, the core of paleoanthropology is also coming to accept the idea that the hominids include at least some if not all of the living great apes and their fossil relatives. Most paleoanthropologists and nearly all molecular systematists however, now agree on key aspects of the pattern of evolution among great apes and humans.

WHAT IS AN ORANGUTAN, ANYWAY?

Darwin (1871) suggested that orangutans represent a separate lineage within the great apes and humans, based on comparative anatomy and biogeography. Later Nuttal (1904) reached the same conclusion based on biochemistry. Despite this, for most of the first two-thirds of the twentieth century, orangutans were grouped with African apes, and sometimes even with hylobatids, in the Pongidae (Schultz, 1963; Simpson, 1945; Pilbeam, 1969). It is nearly universally accepted now that this is not the case. As noted above, Goodman (1963) and later Sarich and Wilson (1967) showed on the basis of immunology that African apes are more closely related to humans than they are to orangutans. While there have been a few studies suggesting either that the pongids really do form a monophyletic group (Kluge, 1983) or that orangutans are actually more closely related to humans than are African apes (Schwartz, 1984), these proposals have not withstood further testing, and have been rejected even by some former advocates (e.g., Schwartz, 1990). The vast majority of molecular and morphological research on this topic has repeatedly confirmed the conclusion linking humans to African apes to the exclusion of orangutans (summarized in Andrews & Cronin, 1982; Groves, 1986; Andrews, 1987; Goodman et al., 1994; Ruvolo, 1994; Easteal et al., 1995).

Orangutans are quite distinct from other hominids as measured either by their morphology or their molecules. This suggests that the amount of time that has elapsed since the divergence of the orangutan lineage from that of other hominids has been relatively great. The fossil record provides a relatively clear indication of a minimum of 13 ma (mega-annum, or, million years) of separate evolutionary history for the orangutan (Pilbeam, 1982; Andrews and Cronin, 1982; Kappelman, et al., 1991). This is the approximate age of the oldest member of the orangutan lineage or clade, *Sivapithecus*. Recently some doubt has been cast on whether or not *Sivapithecus* is indeed more closely related to orangutans than to any other hominid (Röhrer-Ertl, 1988; Pilbeam et al., 1990; Pilbeam, 1996), but most analyses of fossil data continue to support this link (Alpagut et al., 1997; Ward, 1997; Begun et al., 1997). 13 ma is a minimum age for the orangutan clade, which could be considerably older. Since 13 ma is widely used as a calibrating date for molecular clocks[4] (Horai et al., 1992, 1995; Bailey et al., 1992;

Adachi & Hasegawa, 1995; Easteal et al., 1995; Kim & Takenaka, 1996), the divergence times suggested by these analyses must be regarded as minimum estimates. This point is particularly relevant to interpretations of the divergence times of African apes and humans, some of which are much younger than the fossil evidence suggests (Easteal et al., 1995; see below).

A minimum of 13 million years of separate evolution in the orangutan clade may help to explain the large amount of genetic diversity in living orangutans. Morphologically, Bornean and Sumatran orangutans (*Pongo pygmaeus pygmaeus* and *Pongo pygmaeus abelii*) are very similar to one another but not identical (reviewed in Groves, 1986). It is not too difficult to distinguish among the two subspecies in cranial metrics (given relatively large samples) nor is it difficult to identify living individuals by subspecies (Groves, 1986). Though they more closely resemble one another than do bonobos and chimpanzees (*Pan paniscus* and *Pan troglodytes*), the genetic differences between Sumatran and Bornean orangutans are equal to or greater than those that distinguish the two species of *Pan*, according to most accounts (Lucotte and Smith, 1982; Ferris, Brown, Davidson, & Wilson, 1981; Bruce & Ayala, 1979; Groves, 1986; Courtenay, Groves, & Andrews, 1988; Caccone & Powell, 1989; Janczewski, Goldman, & O'Brien, 1990; Ruvolo, 1994). This has prompted Groves (1993) to wonder about the possible advisability of recognizing two separate species of orangutan. Noting that intra-subspecific differences may be as great as those between the subspecies, Groves (1993) rejects this option for the moment. If nothing else, the discrepancy between genetic and morphological differences between orangutan subspecies indicates some de-coupling of the rates of change in these systems, a phenomenon noted long ago in other hominid taxa (e.g., King & Wilson, 1975). In the final analysis, it is very clear from nearly all lines of evidence that orangutans have a long period of evolutionary history independent of other hominids, a point to be considered when assessing the morphological, genetic, and behavioral differences among living great apes, or the lack thereof.

HOW ARE AFRICAN APES AND HUMANS RELATED TO ONE ANOTHER? PART 1: WHERE DO HUMANS FIT IN?

Molecular approaches

While there is nearly universal agreement on the monophyly of the African apes and humans, there remains some disagreement on relations within this clade. This situation is changing, however. Up to about 1994 there were a significant number of systematists who suggested that the gorilla–chimpanzee–human trichotomy could not be or has not yet been resolved (Groves, 1986, 1989; Marks, Schmid, & Sarich, 1988; Holmquist, Miyamoto, & Goodman, 1988; Maeda, Wu, Bliska, & Reneke, 1988; Groves and Patterson, 1991; Ellis et al., 1990; Kawamura et al., 1991; Marks, 1992; Ruano, Rogers, Ferguson-Smith, & Kidd, 1992; Rogers, 1993; Retief et al., 1993). Among those systematists who felt the trichotomy could be resolved, most preferred a chimpanzee–

[4] Clocks that use rate and amount of genetic change between lineages to determine divergence times (see Easteal, et al., 1995 for detailed discussion).

human clade (Brown, Prager, Wang, & Wilson, 1982; Goodman, Braunitzer, Stangl, & Schrank, 1983; Sibley & Alquist, 1984, 1988; Sibley Constock, & Alquist, 1990; Slightom, Chang, Koop, & Goodman, 1985; Miyamoto, Slightom, & Goodman, 1987; Hasegawa, Kishino, & Yano, 1987; Savatier et al., 1987; Ueda et al., 1989; Caccone & Powell, 1989; Gonzalez, et al., 1990; Galili & Swanson, 1991; Ruvolo et al., 1991; Bailey et al., 1992; Begun, 1992a; Horai et al., 1992; Kawaguchi, O'hVigin, & Klein, 1992; Perrin-Pecontal et al., 1992). The smallest number of systematists were those who preferred a chimp–gorilla clade (Ferris, et al., 1981; Templeton, 1983; Hixon & Brown, 1986; Andrews & Martin, 1987; Smouse & Li, 1987; Djian & Green, 1989).[5] However, it is also the case that many of the systematists who expressed a preference in resolving this dichotomy felt that the issue was not fully resolved, and that more evidence would be needed to increase confidence in their conclusions. In essence, then, most molecular systematists up to about 1994 had published that the issue was still unresolved, although more were willing to go out on a limb and favor a chimpanzee–human clade than were willing to favor a chimpanzee–gorilla clade. Although 2 morphological analyses found some evidence for a chimpanzee–human clade (Groves, 1986; Begun, 1992a), few morphologists, including Groves himself (Groves, 1986, 1989; Groves & Patterson, 1991) had much confidence in this conclusion. Most followed Andrews and Martin (1987) and Andrews (1992) in uniting the African apes to the exclusion of humans, based primarily on the shared occurrence of certain details of enamel structure and characters related to knuckle-walking. One exception was Pilbeam (cited in Caccone and Powell, 1989), who suggested that these features may have been secondarily lost in humans, but present in our ancestors. This idea was developed in more detail independently in Groves and Patterson (1991) and Begun (1992a) (see below). Since that time, the molecular systematists have come closer to a consensus (indeed, a consensus is claimed by many already!), and more morphologists are inclined to agree as well. That is, an increasing number of researchers are coming to the conclusion that a chimpanzee–human clade is the most likely (see below).

Two major changes in molecular systematics seem to be responsible for the more consistent results that are beginning to emerge on the question of African ape–human relations. The first is the more widespread use of new techniques (principally PCR [polymerase chain reaction], for DNA amplification) that makes it much easier to sequence nuclear genes, mitochondrial genes, and even entire mitochondrial genomes.[6] This led to a plethora of new sequence data. The second is the now more-or-less universal application of cladistic methods to determine phylogenetic relations from genetic data. Previously the strongest support for a chimpanzee–human clade came from the DNA hybridization data (Sibley & Alquist, 1984, 1987), though these have been

[5] These citations exclude chromosome studies, which have produced widely divergent results, and which have been criticized recently (Borowik, 1995).

[6] Molecular systematists can now determine the sequence of nucleotides that make up the genetic code of DNA in the nucleus, inherited from both parents, as well as the DNA in mitochondria, an organelle within the cell, inherited only from the mother (sperm, though they have mitochondria, do not pass them on during fertilization of the egg). This difference in inheritance accounts in part for the differing rates at which mitochondrial and nuclear DNA evolve.

criticized for methodological shortcomings (Marks et al., 1988; but see Sibley et al., 1990). Caccone and Powell (1989), however, reached the same conclusion from the DNA hybridization data in an analysis considered more reliable (Ruvolo, 1994). Unfortunately, DNA hybridization data are not amenable to cladistic analysis, since the results produce a measure of overall difference rather than discovering discrete "character" differences (Andrews, 1987). When Andrews (1987) attempted to carry out a cladistic analysis of the few molecular data sets that could be analyzed in this way at that time, his results were mixed, and overall he found studies favoring a chimpanzee–human clade unconvincing. In the intervening years, all sequence data (proteins, nuclear DNA, ribosomal RNA, mitochondrial DNA) have been analyzed cladistically.

A number of recent sequence data analyses are quite unambiguous in supporting a chimpanzee–human clade. Goodman et al. (1994) reviews and reanalyzes previous work, primarily that of Bailey et al. (1992), concluding that the chimpanzee–human link is very strong based on the β-globin gene cluster. Their reanalysis of other sequence data, including 10 different nuclear genomic regions (in addition to the β-globin gene cluster), 1 RNA sequence, and 2 mitochondrial DNA (mtDNA) sequences, offers strong support for the chimpanzee–human clade, with many more parallelisms being required to support a chimpanzee–gorilla clade (Goodman et al., 1994, Table 1.1). These authors recognize significant amounts of homoplasy in these data, and interpret it as an indication that the separation of gorillas from the common ancestor of chimpanzees and humans occurred close in time to the separation of chimpanzees and humans.

Ruvolo and colleagues (Ruvolo, 1994, 1995; Ruvolo et al., 1994) also offer strong and convincing evidence for a chimpanzee–human clade. This work, based primarily on mitochondrial cytochrome oxidase subunit (COII) sequences, takes more account of variability with the inclusion of between 4 to 6 African ape individuals in the sample. All the hominoid individuals cluster by taxon, and chimpanzees also cluster with humans to the exclusion of gorillas (Ruvolo, 1994; Ruvolo et al., 1994). This study also includes 4 bonobos, which cluster with chimpanzees, supporting the monophyly of *Pan*. Ruvolo (1994) also considers other molecular studies that fail to support a chimpanzee–human clade, or that support one but only weakly. She points out, as have others (Goodman et al., 1994; Easteal et al., 1995), that in many instances the genes under study have changed too slowly to allow for a resolution of the African ape–human clade. There is, in fact, substantial evidence to suggest significant amounts of variability in the rate at which different parts of the nuclear and mitochondrial genomes change through time (Chang and Slightom, 1984; Goodman, Koop, Czelusnaik, & Weiss, 1984; Vawter & Brown, 1986; Li & Tanimura, 1987; Hasegawa et al., 1987; Hayasaka, Gojobori, & Horai, 1987; Miyamoto et al., 1987; Holmquist et al., 1988; Maeda et al., 1988; Djian & Green, 1989; Perrin-Pecontal et al., 1992; Horai et al., 1992, 1995; Retief et al., 1993; Ellsworth, Hewett-Emmet, & Li, 1993; Deeb et al., 1994; Livak, Rogers, & Lichter, 1995; Adachi & Hasegawa, 1995; Ruvolo, 1995; Easteal et al., 1995; Mohammad-Ali, Eladari, & Galibert, 1995; Queralt et al., 1995; Nachman, Brown, Stoneking, & Aquadro, 1996; Arnason, Xiuteng, & Gullberg, 1996; Kim & Takenaka, 1996). Mohammad-Ali et al. (1995) also reject the results of an analysis that failed to support a

chimpanzee–human clade based on rate variability. In this case, it was the work of Oetting, Stine, Townsend, and King, (1993), who found support for a human–gorilla clade based on their analysis of tyrosinase-related genes. Mohammad-Ali et al. (1995) suggest that the relatively short nucleotide sequence analyzed by Oetting, et al. (1993) is known to have evolved fast, making the identification of homologous changes at given *loci* very difficult.

A number of other recent studies also support a chimpanzee–human clade from nucleotide sequence data (Perrin-Pecontal et al., 1992; Ueda et al., 1989; Gonzalez et al., 1990; Galili & Swanson, 1991; Horai et al., 1992, 1995; Deeb et al., 1994; Adachi & Hasegawa, 1995; Van der Kuyl, Kuiken, Dekker, & Goudsmit, 1995; Dorit, Akashi, & Gilbert, 1995; Meneveri et al., 1995; Mohammad-Ali et al., 1995; Kim & Takenaka, 1996). In addition to the previously cited work on DNA hybridization in support of this grouping (Caccone & Powell, 1989; Sibley et al., 1990), a cladistic analysis of discrete chromosomal data treating these essentially as morphological character states also supports this conclusion (Borowik, 1995).

Only a few recent molecular studies support a chimpanzee–gorilla clade. As noted above, a larger number fail to resolve the trichotomy, or weakly support either a chimpanzee–gorilla or chimpanzee–human clade, but this is probably related to the rate at which the *loci* evolve, the fact of a relatively close evolutionary relationship among the African apes and humans, and a number of other methodological and/or theoretical constraints (Hasegawa et al., 1987; Ruvolo, 1994, 1995). Although the work of Djian and Green (Djian & Green, 1989; Green & Djian, 1995), Livak et al. (1995), Queralt, et al. (1995), and Ellis, et al. (1990) (in part) has been used to argue in favor of a chimpanzee–gorilla clade, in 3 of the 4 studies, the authors make a distinction between gene trees and phylogenetic trees,[7] and are unwilling to strongly support a particular phylogeny. Livak et al. (1995), for example, conclude that the chimpanzee dopamine D_4 receptor gene sequence is closer to that of gorillas than to humans. However, they suggest that because this is incongruent with other sequence data (see above), the divergences among the three great apes must have occurred very close in time (see also Rogers [1993]). This suggestion is not inconsistent with other conclusions that nevertheless support a chimpanzee–human clade (Goodman et al., 1994). Ellis et al. (1990) found X-chromosome pseudoautosomal boundary sequences more similar between chimpanzees and gorillas, while finding Y-chromosome pseudoautosomal boundary sequences to be more similar between chimpanzees and humans. Although this result is ambiguous, these authors also point out that the total number of position synapomorphies in all sequences shared by humans and chimpanzees is 4, whereas only 2 are shared by chimpanzees and gorillas. While not very strong, overall this data would tend to support a chimpanzee–human clade as well. Queralt et al. (1995), who also found a

[7] Gene trees, like character trees, provide evidence for relationships based on individual *loci* or characters. Phylogenetic trees should combine data from more than one *locus* or from many characters. They depict relationships supported by the largest number of *loci* or characters. Those *loci* or characters that link taxa in a pattern of relationship different from the phylogenetic hypothesis are deduced to be homoplasies, having evolved independently in the separate lineages that share them.

closer link between chimpanzees and gorillas than between chimpanzees and humans, nevertheless fail to find support for a chimpanzee–gorilla clade, again citing the need for many more genes. The same research group previously reported an analysis of the same primate sequences (Retief et al., 1993) in which a human–gorilla link was supported. The main difference between the two studies was the inclusion of nonprimate data in the 1995 paper. It should also be noted that these same analyses grouped marmosets with green monkeys (Retief et al., 1993) and gibbons with African apes and humans to the exclusion of orangutans (Queralt et al., 1995), thus contributing to the uncertainty regarding the exact phylogenetic significance of these results.

The only analysis so far that claims an unambiguous linkage between chimpanzees and gorillas is the involucrin gene sequence data of Djian and Green (1989). These authors (Djian & Green, 1989; Green & Djian, 1995) claim that the involucrin gene data is particularly well suited to resolving relationships among very closely related hominoids because of its rapid rate of change.[8] Ruvolo (1994) disagrees with this conclusion. She argues that the segment of the involucrin gene sequence that links chimpanzees to gorillas, the "modern" repeat region, is susceptible to a number of molecular evolutionary processes that may cause it to generate an unreliable phylogeny. There has been no resolution to this disagreement (Green & Djian, 1995; Ruvolo, 1995). As noted earlier, because of the likelihood that individual gene trees will not always correspond to phylogenetic trees due to homoplasy, the greater the number of genes analyzed, the more likely a consensus will emerge (Ruvolo, 1994, 1995; Stewart, 1993; Queralt et al., 1995; Retief et al., 1993; Maeda et al., 1988; Pamilo & Nei, 1988). Even if the gene tree for involucrin does link gorilla and chimpanzee sequences, it is still in the significant minority compared to those that link humans to chimpanzees.

A few researchers are particularly concerned with the issue of intraspecific variability in sequence data (polymorphism), and in the related issue of homoplasy (Rogers, 1993; Rogers & Comuzzie, 1995; Marks, 1992, 1994). Marks (1994), for example, points out that a great deal of homoplasy exists in the nuclear DNA sequence data if a chimpanzee–human clade is accepted, but much less with a chimpanzee–gorilla–human trichotomy. However, more fully resolved phylogenetic trees (trees with as many dichotomous branchings as possible) are usually more homoplasious than are less fully resolved trees. By definition, collapsing separate branches into a single origin will decrease contradictory data, because much of the data is, in fact, ignored. For example, collapsing the orangutan branch into the African ape and human branch, making orangutans, African apes, and humans unresolved, decreases the amount of homoplasy by the number of homoplasies in the orangutan clade, and there are many (Begun & Guleç, 1998). This does not mean that an African ape–orangutan–human trichotomy is a better explana-

[8] The claim that gene sequences evolve too rapidly, too slowly, or at just the right rate to be helpful in analyzing particular relationships (e.g., Ruvolo, 1994; Mohammad-Ali, et al., 1995; Djian & Green, 1989) may seem overly convenient and is difficult to prove, but it mirrors similar claims about anatomical regions and their phylogenetic significance (e.g., Begun, 1995). It is clear that, depending on the rate of change and the time since divergence, some sequences will be more useful than others for resolving particular relationships, in the same way that some isotopes are more useful than others in calculating absolute ages, depending on decay rates and geologic time.

tion. Because more data support a specific resolution, it just means that there is a lot of homoplasy. In other words, trichotomies result in less homoplasy than dichotomies for methodological reasons; a priori assumptions about the amount of homoplasy resulting from the evolutionary process are neither necessary nor desirable.

Marks (1992, 1994) shares with Rogers (1993) and Rogers and Comuzzie (1995) a more serious concern about polymorphism and the possibility that, by chance alone, different alleles could find themselves distributed among descendant populations in a pattern that differs from the actual evolutionary relations among those descendant populations (see Rogers, 1993 and Marks, 1992 for a comprehensive discussion of this problem). Concern about polymorphism has been widely expressed in the molecular literature (Ruvolo, 1994, 1995; Pamilo & Nei, 1988; Wu, 1991). This is one of the main reasons for the widespread recognition that a gene tree may be different from the species tree (see above), and it holds for morphological data as well, in the distinction between a single-character tree and a phylogeny based on many characters (Begun, 1994b). Rogers (1993) and Marks (1992) both make the claim that the chimpanzee–human–gorilla trichotomy is unresolvable or difficult to resolve currently because of the confounding influence of polymorphism. Rogers (1993) and Rogers and Comuzzie (1995) recognize that the evidence of a chimpanzee–human clade is stronger, i.e., supported by a larger number of genetic *loci*, but suggest that the number of contradictory *loci* indicate a very short time between the gorilla divergence and the chimpanzee–human divergence, a conclusion essentially in agreement with Goodman et al. (1994). In the final analysis, more nucleotide positions support a chimpanzee–human clade than any other single clade, as noted by Goodman, et al. (1994), and for this reason this clade is to be preferred, regardless of the amount of homoplasy implied.

Finally, one last objection to the results of molecular systematics commonly expressed by anthropologists is that the number of individuals sampled by molecular systematists is very small, leading to the possibility that the gene sequence discovered may not be representative of the species as a whole (Marks, 1994; Ruvolo, 1995). However, as Ruvolo (1994) clearly shows, based on the theoretical work of Takahata (1989), increasing the number of individuals will not increase the reliability of a gene tree, because the polymorphism that exists today does not reflect ancestral polymorphism. Modern alleles are, in fact, more likely to have evolved from a single ancestral allele following coalescence of ancestral polymorphisms. This point is also made strongly by Pamilo and Nei (1988) and Wu (1991). So, although ancestral polymorphism can confound a phylogenetic analysis when the divergence times are short, larger sample sizes of modern hominoids will not help resolve this difficulty.[9]

Though genes clearly do not evolve at the same rates, and a number also probably do

[9] Because descendant populations tend to represent only a small percentage of the original genetic diversity of the ancestral species, most ancestral polymorphism will not be represented in a descendant population. Ancestral polymorphisms may only be represented by a single allele in a descendant population. However, even if more than one allele is passed on to a new species, since allelic frequencies fluctuate between 0% and 100%, ancestral polymorphic *loci* will eventually coalesce to a single allele, from which subsequent variation in the descendant species will evolve. The longer the time since separation between species, the less likely they will be to share ancestral polymorphisms.

not evolve at a constant or predictable rate (Zuckerkandl & Pauling, 1962; Sarich & Wilson, 1967; Miyamoto et al., 1987; Ellsworth et al., 1993; Ruvolo, 1995; Nachman et al., 1996; Kim & Takenaka, 1996), studies have shown that some gene sequences and some DNA hybridization data can be used to estimate times of divergence based on amounts of difference among the taxa analyzed (Sibley et al., 1990; Hasegawa et al., 1987; Hayasaka et al., 1988; Caccone & Powell, 1989; Ruvolo, 1994, 1995; Adachi & Hasegawa, 1995; Easteal et al., 1995; Horai et al., 1992, 1995).

There are basically two schools of thought on this issue with regard to African ape–human relations. One holds that the divergence between gorillas and the ancestor of chimpanzees and humans was very close to that between chimpanzees and humans, while the other holds that it was further away. As previously noted, Rogers (1993) and Rogers and Comuzzie (1995) suggest that the degree of incongruity in sequence data results suggests that the divergence times were very close together. In fact, though both Rogers (1994) and Marks (1994) concede that humans and chimpanzees may share a most recent common ancestry, both believe that the divergence times among the three are so close together that molecular data may never be adequate to resolve the issue. For both authors, if the time between the divergence of the gorilla and that between chimpanzees and humans is less than about 1 ma, then the molecular data may prove inconclusive. It is ironic that the paleontological data may, in fact, be more useful in this instance. Morphological change in lineages of many mammals are quite distinguishable within time ranges well under 1 ma. In fact, in rapidly evolving lineages such as Pleistocene rodents, differentiation is detectable within 0.1 ma. Even within hominoids, there is obvious evolutionary change within 0.5 ma intervals among the australopithecines and within the genus *Homo*.

Goodman et al. (1994) also believe that divergence times among the African apes and humans were close, based on the overall degree of similarity of the three genera and the amount of homoplasy in the data. Easteal et al. (1995) also place the divergences of gorillas, humans, and chimpanzees very close together, though they support the chimpanzee–human clade. These authors are so impressed with the overall genetic similarity of the African apes and humans that they advocate placing them all, along with all fossil humans, in the genus *Homo*. In contrast to these studies, Ruvolo (1994, 1995) provides evidence for a substantial period of separation of the chimpanzee–human and gorilla clades, based both on results using mtDNA and her interpretation of the DNA hybridization results of Caccone and Powell (1989). The very recent work of Kim and Takenaka (1996), finding about twice the amount of difference between gorillas and the chimpanzee group as between chimpanzees and humans in the Y-chromosomal TSPY gene sequence, also suggests a substantial separation between the two events. To these conflicting interpretations can be added the conclusions of researchers advocating a molecular-clock approach.

The earliest molecular-clock estimates produced a divergence-time estimate between chimpanzees and humans of roughly 5 ma (Sarich & Wilson, 1967), based on protein immunodiffusion. There has been a great deal of discussion of these results in the molecular and paleontological literature, much of which is beyond the scope of this

Table 1.2 *Recent hominid divergence times estimates*

Research	Orangutan	Gorilla	Chimp–Human	Chimp–Bonobo
Sequence data				
Nuclear DNA				
Hasegawa et al. (1987)	9–15	4.1–7.8	3.1–7.0	
Easteal et al. (1995)	7.3–9.8	*c.* 5	3.2–4.5	
Holmes et al. (1988)	14.5[a]	16.2–9.2	5.9–8.9	1.9–4.4
mtDNA				
Adachi and Hasegawa (1995)	13–16[a]	7–9[b]	4–5	2–3[b]
Horai et al. (1995)	13[a]	6.3–6.9	4.7–5.1	2.1–2.5
Hybridization data				
Sibley and Alquist (1987)	13–17[a]	7.7–11	5.5–7.7	2.4–3.4
Caccone and Powell (1989)12–16[a]	6–8			
Ruvolo (1995)		7.4–8.9	5–6	
Paleontology[c]	13–16		> 4.4	

Dates in millions of years. See text for discussion.
[a] Age given by authors using paleontological data.
[b] Applying the rough correction used by the authors on their chimpanzee–human divergence estimate.
[c] Data from Kappelman et al. (1991), Cande and Kent (1995) and WoldeGabriel et al. (1994).

chapter. More recently, as noted above, a large number of studies have supported the notion of a molecular clock on empirical and theoretical grounds for DNA hybridization and nucelotide sequence data. The most recent of these are reviewed here.

Sibley and Alquist (1987) estimated times of divergence within the African apes and humans using DNA hybridization data. They estimated the time of divergence between gorillas and the chimpanzee–human ancestor to be between 7.7 and 11 ma, and that between humans and chimpanzees to be between 5.5 and 7.7 ma (Table 1.2). This was based on the assumption that the relationship between time and overall average DNA divergence is linear within hominoids, and a calibration range using fossil evidence to date the first appearance of the orangutan lineage (13–17 ma) and the first appearance of the cercopithecoid lineage (25 ma). Caccone and Powell (1989), in an analysis generally accepted as the most sophisticated DNA hybridization work on hominoid relations (Ruvolo, 1995), obtain essentially the same results based on the same assumptions.

Other divergence dates provided recently are based on DNA sequences. Hasegawa et al. (1987) used data from the η globin pseudogene (a gene that does not code for a functional polypeptide) to provide 95% confidence intervals for the divergence dates, yielding about 9–15 ma for the orangutan divergence, 4.1–7.8 for that of the gorilla, and 3.1–7.0 for that of humans and chimpanzees. This was based on an estimate of 38 ma for the divergence of platyrrhines and catarrhines, based on the fossil record. These authors

also note that their estimates of great ape–human divergence times may be too recent, given evidence they find of a rate of slowdown in the Hominoidea. Nevertheless, in another study, Hasegawa et al. (1990) found an even later date of 3.2–4.6 ma for the divergence between chimpanzees and humans, and 4.3–5.9 ma for that of the gorilla, based on a short sequence of mtDNA. In their most recent reanalysis, Adachi and Hasegawa (1995) obtain dates of 3.0–4.2 ma for divergence between chimpanzees and humans, 5.1–6.5 for gorilla, and 1.4–2.2 for the two species of *Pan*, assuming a divergence time of 13–16 ma for orangutans. However, as earlier, they note that these dates may be too recent given evidence of rate variation. In the final analysis, they conclude that a reasonable estimate for the human–chimpanzee divergence would be 4–5 ma.

Horai et al. (1992) also used mtDNA sequence data to obtain a divergence estimate of 4.2–5.2 ma for chimpanzee–humans, 7.0–8.4 ma for gorillas, and 2.0–3.0 for bonobos and chimpanzees, again assuming a divergence time of 13 ma for orangutans, from the fossil record. Although their analysis of evolutionary relations among hominoids was based on a long sequence of mtDNA, they chose to estimate divergence times based on a subset of these data containing relatively conservative sequences. This was to avoid including too many different genes, possibly evolving at different rates, and also to avoid including portions of the sequence that have evolved more rapidly and may have undergone changes that are not detectable. Their results overall are quite compatible with those of Hasegawa and colleagues (see above), though these authors have suggested that the results of Horai et al. (1992) give divergence times that may be too old, for a number of methodological reasons (Adachi & Hasegawa, 1995). In a more recent refinement of their work, based on a larger portion of the mtDNA sequence, Horai et al. (1995) estimated the divergence times at 6.3–6.9 for gorilla, 4.7–5.1 for human–chimpanzee, and 2.1–2.5 for chimpanzee–bonobo, again calibrating based on an orangutan divergence of 13 ma. The gorilla divergence is slightly closer to that of humans and chimpanzees compared to their previous analysis, but otherwise their results are similar to other work (Table 1.2).

In the most recent and most intriguing work, Easteal et al. (1995) cite a range of dates from 2.5–6.0 ma for the divergence of humans and chimpanzees, based on a review of both hybridization and sequence data (gorillas are not included in their analysis). The ages they obtain are compatible with those of previous researchers when they use the same estimates of base substitution rates, but they also make the case that these rates should be higher than generally accepted, at least within the Hominoidea (Easteal et al., 1995). In fact, the range of rates they prefer gives an estimate of the date of divergence of chimpanzees and humans between 3.2 and 4.5 ma. However, their preference for these rates is based on their conclusion that DNA evolution proceeds at the same rate in all mammals, and that these ranges result in divergence estimates that are the least incompatible with paleontological data for other mammalian divergences. These results contrast with the work of both Sibley and Alquist (1987) on DNA in general, and Goodman et al. (1983) on protein coding sequences, which demonstrate significantly different rates in different mammalian